
Two New Species of *Hybanthus* (Violaceae) from Central America and a Regional Key for the Genus

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ABSTRACT. Two morphologically and ecologically distinctive, woody *Hybanthus* species from Central America are described, illustrated, and mapped. *Hybanthus denticulatus* inhabits lowland rainforest from northern Nicaragua to eastern Panama and is allied to Mexican and Guatemalan *H. elatus*. *Hybanthus hespericlivus* is restricted to mid-elevation forest on the western mountain slopes of northern Costa Rica and resembles Panamanian *H. jefensis* and northern Mesoamerican *H. sylvicola*. A key to Central American species of *Hybanthus* is provided.

Systematic and nomenclatural studies of Mexican and Central American Violaceae for several flora projects, including the "Manual de Plantas de Costa Rica" and "Flora Mesoamericana," have resulted in the discovery of two new species of *Hybanthus* commonly misidentified as *H. guanacastensis* Standley, a species of higher-elevation forest in northern and eastern Costa Rica. Both new species resemble *H. guanacastensis* and other members of *Hybanthus* subg. *Hybanthus* in their woody habit and axillary short shoots with one or more peduncles. However, their strongly zygomorphic flowers, with the bottom petal at least twice as long as the lateral and upper ones and strongly differentiated into a slender claw and greatly expanded

blade, and free filaments of the stamens, suggest instead an alliance to subgenus *Ionidium* (Ventenat) Schulze-Menz. The infrageneric relationships of the new species are as yet unresolved.

Morton was the last to revise the genus *Hybanthus* in Mexico and Central America, through synoptical and piecemeal efforts (Morton, 1944, 1971). While he initially provided a pared-down key for herbaceous and semi-herbaceous species that he recognized in 1944, he left out woody shrubs and treelets in this earlier key and never published a more inclusive key in subsequent works in which he recognized additional species of *Hybanthus*. Exacerbating the situation are several names used in publications by Morton and his contemporaries that the first author has determined are synonyms. Since Morton's time, no single key or taxonomic resource has been available for *Hybanthus* species of Mexico and Central America. Consequently, approximately 25% of *Hybanthus* specimens from this region are misidentified. A treatment of *Hybanthus* for the entire region will be published in "Flora Mesoamericana" several years in the future. In the interim the following key will facilitate identification of dried flowering Central American specimens of *Hybanthus*. Synonyms in brackets represent names recognized as distinct species by Morton (1944, 1971).

KEY TO THE SPECIES OF *HYBANTHUS* IN CENTRAL AMERICA

- 1a. Stems predominantly or entirely herbaceous; plant 0.1–0.5 m tall.
 - 2a. Corollas 20–35 mm long; sepal margins dentate; plant densely and coarsely long-hirsute throughout *H. calceolaria* (L.) Schulze-Menz
 - 2b. Corollas 9–17 mm long; sepal margins entire; plant glabrous or pubescent but not densely and coarsely long-hirsute throughout.
 - 3a. Leaf blades 3.2–8.0 times as long as broad; at least the lowest leaf nodes opposite (lower leaves deciduous on *H. attenuatus*).
 - 4a. Upper leaves alternate; leaf blades broadly lanceolate, widest at middle, tapering gradually to a cuneate or slightly convex base . . . *H. attenuatus* (Humboldt & Bonpland) Schulze-Menz

- 4b. All leaves opposite; leaf blades narrowly linear-acuminate, widest near the abruptly truncate base *H. oppositifolius* (L.) Taubert
- 3b. Leaf blades up to 2.5 times as long as broad; all leaf nodes alternate.
- 5a. Leaf blades elliptic, widest at the middle, 2.0–2.5 times as long as wide; stem pubescence incurved and ascending *H. thiemei* (F. Donnell Smith) C. V. Morton [*H. longipes* Dowell]
- 5b. Leaf blades broadly obovate, widest above the middle, up to 1.5 times as long as wide; pubescence straight and spreading *H. verbenaceus* (HBK) Loesener
- 1b. Stems completely woody; plant 0.5–6.0 m tall.
- 6a. Corollas 3–9 mm long, weakly zygomorphic, the bottom petal 1.1–1.3 times as long as lateral ones, not strongly differentiated into a slender claw and greatly expanded blade.
- 7a. Flowers many in pedunculate cymes; stems often thorny *H. yucatanensis* Millspaugh
- 7b. Flowers solitary or in few-flowered glomerules; stems unarmed.
- 8a. Leaf blades lance-ovate to ovate-elliptic, sharply acute at apex, margins irregularly and coarsely (sometimes doubly) serrate *H. guanacastensis* Standley
- 8b. Leaf blades oblanceolate to narrowly obovate, obtuse to rounded at apex, margins crenate to subentire *H. mexicanus* Gingins [*H. costaricensis* Melchior]
- 6b. Corollas 7–45 mm long, strongly zygomorphic, the bottom petal 1.5–2.0 times as long as lateral petals, differentiated into a slender claw and a greatly expanded blade.
- 9a. Petioles 10–30 mm long; leaf blades widest near the symmetrically broadly rounded base *H. galeottii* (Turczaninow) C. V. Morton
- 9b. Petioles 1–5 mm long; leaf blades widest near the middle, cuneate or asymmetrically subtruncate to narrowly rounded at the base.
- 10a. Flowers 35–45 mm long; leaf blades coarsely and irregularly serrate *H. prunifolius* (Humboldt & Bonpland) Schulze-Menz
- 10b. Flowers 7–18 mm long.
- 11a. Leaf blade margins uniformly serrulate, crenulate or denticulate with 35 or more teeth on each side; stipules 3–12 mm long.
- 12a. Leaf margins denticulate; young leaves membranous and translucent; northern Nicaragua to eastern Panama *H. denticulatus* H. E. Ballard, M. A. Wetter & N. Zamora, sp. nov.
- 12b. Leaf margins crenulate; young leaves thick; Mexico and northern Guatemala *H. elatus* (Turczaninow) C. V. Morton [*H. brevis* (Dowell) Standley, *H. chiapasiensis* Lundell]
- 11b. Leaf blade margins subentire to remotely low-serrate or crenate with up to 20 teeth on each side; stipules to 2 mm long.
- 13a. Leaf blades with (5–)6–8 major lateral veins on each side, sharply acuminate at tip; stipules pale; southern Mexico to Belize and northern Honduras *H. sylvicola* Standley & Steyermark
- 13b. Leaf blades with 3–4(–5) major lateral veins on each side, rounded at very tip; stipules brown or tinged with red-brown; Costa Rica and Panama.
- 14a. Leaves green on both sides; corollas (9–)11–13 mm long; northwestern Costa Rica *H. hespericlivus* H. E. Ballard, M. A. Wetter & N. Zamora, sp. nov.
- 14b. Undersides of leaves with fine red-brown punctae and reticulations; corollas 7–10 mm long; central Panama *H. jefensis* Todzia

Hybanthus denticulatus H. E. Ballard, M. A. Wetter & N. Zamora, sp. nov. TYPE: Costa Rica. Osa: Uvita de Osa, Distrito Bahía Ballena, bosque atrás de casa de León González, cerca a la Quebrada Curingo, 9°09'5"N, 83°43'35"W, 20 Dec. 1992, N. Zamora 1912, B. Hammel, R. Aquilar & A. Fernández (holotype, WIS; isotypes, CR, INB, MO, US). Figure 1A–D.

Habitus suffruticosus petalum infimum unguiculatum petalis summis et lateralibus suo duplo longius vel paulo longius folia acuminata dentibus numerosis, characteribus *H. elatus* (Turczaninow) C. V. Morton simile sed foliis latioribus denticulatis basi obtusa ad truncatam junioribus membranaceis ab ea recedens.

Spreading few-stemmed shrub or treelet arising

from a rhizome, to 6 m tall and 10 cm diam. at the base, stems entirely woody, sparsely to moderately branched, branches villosulous near the tips. Leaves alternate, young blades at the tips of branches membranous and translucent, glabrate or glabrous, the fully expanded ones thin but opaque, glabrous, at maturity 4.5–16.3 mm long and 1.7–6.5 mm broad, oblanceolate to obovate-lanceolate, acuminate at the tip, often asymmetrical and typically narrowly obtuse to truncate at the base, major primary veins 6–8, margins typically uniformly denticulate (infrequently serrulate) with sharply acuminate teeth; petioles 2–5 mm long, glabrous to sparsely villous; stipules 3–12 mm long, free, tan to ivory, lance-acuminate, thickly keeled, the keel exerted as an apical awn, minutely erose along the

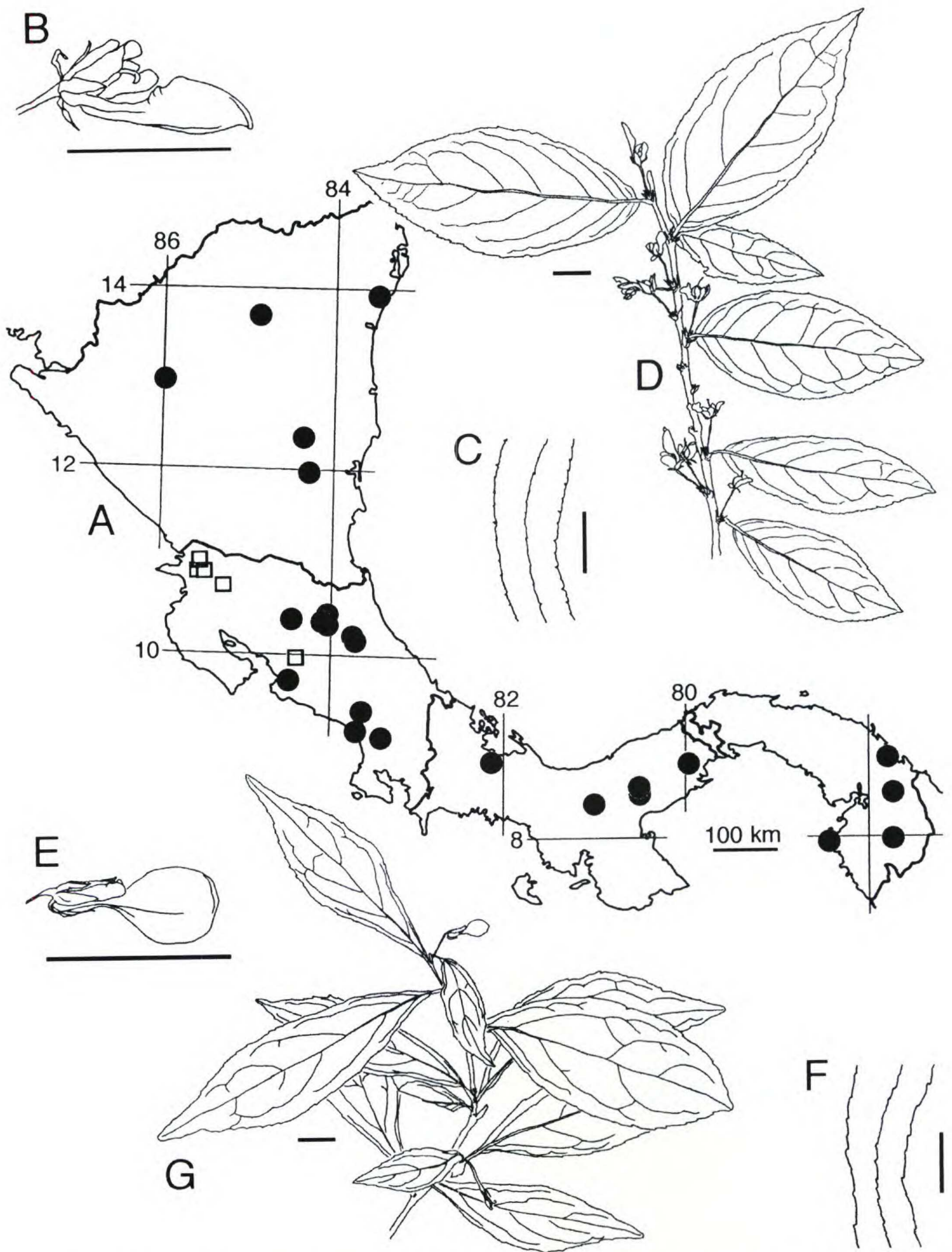


Figure 1. —A. Ranges of *Hybanthus denticulatus* and *Hybanthus hespericlivus*; closed circles = *H. denticulatus*, open squares = *H. hespericlivus*. B–D. *Hybanthus denticulatus* H. E. Ballard, M. A. Wetter & N. Zamora. —B. Flower. —C. Leaf margins. —D. Habit. Drawn from holotype. E–G. *Hybanthus hespericlivus* H. E. Ballard, M. A. Wetter & N. Zamora. —E. Flower. —F. Leaf margins. —G. Habit. Drawn from holotype. Scale bars = 1 cm. Each symbol may represent two or more proximal collections on the range map.

narrow to broad membranous margins. Inflorescence of 1–2 flowers from axillary short shoots 2–5 mm long; bracts of short shoots similar to stipules but smaller, 1–3 mm long; peduncles 7–21 mm long, jointed above the middle, glabrate to moderately villosulous, bearing a pair of bracteoles ca. 1 mm long near the base; flower 10–16 mm long, strongly zygomorphic; calyx glabrous, sepals 5, 2–5 mm long, narrowly ovate-triangular to lance-acuminate, herbaceous with semi-membranous margins, the lateral pair of sepals slightly larger than the others; corolla white overall, the blade of the bottom petal with a purple blotch near the base just above the juncture with the claw, the claw yellowish within; petals 5, upper ones oblong-lanceolate and rounded at the tip, 4–6 mm long, lateral ones oblong-lanceolate to obpyriform and rounded to truncate at the tip, 5–7 mm long, bottom one 10–16 mm long, at least twice as long as lateral and upper petals, slightly protuberant basally where it surrounds the glandular bottom stamens, narrowed in the basal half as a slender, longitudinally furrowed claw and expanded abruptly and broadly in the apical half to a deltoid-obovate blade 5–9 mm broad, broadly cuneate at the base, mucronate at the tip, the claw sparsely villous inside and glabrous to minutely puberulent near the base outside; style not exerted at anthesis, 3–4 mm long, slender-cylindrical, gradually and uniformly expanding distally, abruptly bent to a short-conic tip; stamens 3–5 mm long, the filament two-thirds as long and one-fourth as broad as the anther proper, the ventral thecae together narrower than the anther body, tipped by an ovate-oblong, orange-brown connective appendage as long as or up to one-third longer than the anther body; the two lowest stamens 20% larger than the other three, on broader filaments bearing a dorsal gland, the dorsum of the anther villous with a tuft of white hairs on each side at the base; capsule narrowly ovoid, 7–12 mm long, glabrous, distinctly veined, green when young but drying tan after dehiscence; seeds 2–3 per valve, 3–4 mm long, obovoid to suborbicular, moderately lustrous, medium to dark brown, lacking an elaiosome.

Habitat and phenology. The denticulate leaf margin, unique among North and Central American *Hybanthus*, provides the specific epithet. This new species is widely distributed in wet lowland forest from sea level mostly to 500 m, rarely up to 1000 m, from northern Nicaragua to the Colombia–Panama border. It flowers primarily from December through May, occasionally as early as October.

Considering its distinctive morphology, wide range, the large number of verified herbarium col-

lections, and much previous work on the genus in Mexico and Central America, both monographic (Dowell, 1906; Lundell, 1968; Morton, 1944, 1971; Schulze-Menz, 1936) and floristic (Robyns, 1967; Standley, 1937), it is remarkable that *H. denticulatus* has been passed over until now. It is similar to *H. guanacastensis* in its woody habit, axillary short shoots bearing flowers and ivory to tan stipules, and has routinely been misidentified as such. Both new species differ strikingly from *H. guanacastensis* in their strongly zygomorphic flowers with very large and well-differentiated bottom petals. The leaves of *H. denticulatus* diverge from those of *H. guanacastensis* in a number of details including distinctly thinner blades (the younger ones especially being membranous and translucent), the uniformly denticulate rather than coarsely and irregularly serrate margins, and the tendency toward more asymmetrically rounded blade bases.

Following the misidentifications of others, Todzia (1989) mistook the present species for *H. guanacastensis* in her comparison of *H. jefensis* and the key to Panama *Hybanthus* species. However, examination of Standley's holotype of *H. guanacastensis*, deposited at US, clearly refers the latter name to the Costa Rican species with small, weakly zygomorphic flowers and irregularly serrate leaves.

The present new species is isolated altitudinally and ecologically from *H. guanacastensis* and *H. hespericlivus* in Costa Rica, growing in wetter tropical forest sites and in most instances at much lower elevations. While it also grows at very low elevations in Panama, *H. denticulatus* ascends to somewhat higher altitudes in the low mountain ranges of northern and western Nicaragua where the other two species are absent. It attains greater stature than either species and approaches the habit of a treelet, often reaching 5–6 m tall and a substantial DBH. It is most similar to *H. elatus*, a woody few-stemmed shrub or treelet of mid-elevation forests from central Mexico to northern Guatemala, but differs from the latter in certain vegetative features indicated in the key as well as a more southern range and a predominantly lowland wet forest habitat.

Paratypes. COSTA RICA. **Alajuela:** Finca Los Ensayos, *Alverson 1996* (CR, MO). **Heredia:** Zona Protectora La Selva, *Schatz & Bockbrader 1039* (CR, DUKE); Zona Protectora La Selva, *Schatz & Fetcher 1057* (CR, F); Zona Protectora, northern slopes Volcán Barba, *Grayum 3118 & Schatz* (DUKE). **Limón:** cerca al Río Toro Amarillo, *Jiménez M. 2814* (CR, F, MO); Bordes Del Río Toro Amarillo, *Jiménez M. 2787* (CR, F); near the Río Toro Amarillo, *Godfrey 66297* (MO); Toro Amarillo, *Lent 314* (F, US). **Puntarenas:** Uvita de Osa, *Zamora 1496*, *Jiménez, González & Gamboa* (CR, K); Orilla de quebrada la Mona,

Soto KR-663 (CR). **San José:** basin of El General, *Skutch 4936* (CR, F); Reserva Biológica Carara, *Zamora 2094 & II Curso de Botánica* (INB, WIS). NICARAGUA. **Mata-galpa:** Salto Santa Emilia, *Sandino 2763* (MO). **Zelaya:** E de Caño Angostura, *Sandino 4633* (DUKE); Caño Hormiguero SE of Cerro la Pimienta number 1, *Pipoly 5053* (DUKE); Caño Zamora on Río Rama, *Stevens 8832* (DUKE); region of Braggman's Bluff, *Englesing 234* (F). PANAMA. **Bocas del Toro:** 8.5 road-miles from bridge near Fortuna Dam on road towards Chiriquí Grande, *McPherson 6749* (CAS, DUKE, US). **Coclé:** New Works at Aseradera Rivera, *Folsom & Robinson 2378* (MO); area around Rivera Sawmill, *Folsom & Page 5971* (MO); El Copé, *Hammel 2377* (MO, US); Atlantic slope of the Continental Divide near sawmill (whiskey) above El Copé, *Knapp & Dressler 3451, 3434* (MO); El Copé, ½ hour walk from sawmill, *Antonio 2083* (MO); near saw-mill, 8 km N of El Copé (28 km NW of Penonome), *Maas, Berg & Dressler 2737* (MO). **Darién:** S of Garachiné near Pacific coast above Casa Vieja, *Hensold 1076* (F); Río Pirre, 10 mi. S of El Real near "Dos Bocas," *Foster 2265 & Lowenbach* (MO, US); Camp Tiotuma, *Duke 15509* (MO); 0.5 to 1.5 mi. E of Manene, *Hartman 12100* (MO); Río Tuquesa, at middle Tuquesa Mining Company camp called Charco Peje, *Mori 7037* (MO); Río Tuquesa, at lower Tuquesa Mining Company camp called Charco Chiva, *Mori 6941* (MO). **Panamá:** Cerro Campana, *McPherson 7906* (WIS). **San Blas:** Hydro Camp Cuadi on Río Cuadi, *Duke 15459* (F, MO). **Veraguas:** NW of Santa Fe, *Mori & Kallunki 5233* (MO).

Hybanthus hespericlivus H. E. Ballard, M. A. Wetter & N. Zamora, sp. nov. TYPE: Costa Rica. Guanacaste: Parque Rincón de La Vieja Liberia, del Puesto Santa María siguiendo el sendero del mirador, subiendo por la fila al noroeste, 10°46'N, 85°18'W, 28 Feb. 1988, G. Herrera 1561 (holotype, WIS; isotypes, INB, MO). Figure 1A, E–G.

Habitus suffruticosus petalum infimum unguiculatum petalis summis et lateralibus suo duplo longius folia oblanceolata remoti-serrata stipulis minutis brunneis, characteribus *H. jefensis* Todzia et *H. sylvicola* Standley et Steyermark affinis, differt a *H. jefensis* foliis multo grandioribus acuminatis maculis rubris carentibus, differt a *H. sylvicola* apicibus foliorum rotundatis venis paucioribus floribus et capsulis grandioribus.

Spreading few-stemmed shrub arising from a rhizome, usually to 1.5 m (rarely to 2 m) tall and 1 cm diam. at the base, stems entirely woody, sparsely to moderately branched, branches finely puberulent near the tips. Leaves alternate, youngest blades at the tips of branches thin and semi-transparent, glabrous, the fully expanded ones opaque, at maturity 3.5–10.3 mm long and 1.3–3.6 mm broad, oblanceolate, abruptly short-acuminate at the tip, long-tapering to the narrowly cuneate base, major primary veins 3–4(–5), margins in the basal third essentially entire and in the apical two-thirds remotely low-serrate with narrowly rounded teeth; petioles 2–6 mm long, glabrous to sparsely puber-

ulent; stipules 0.7–1 mm long, free, tinged with red-brown, lance-triangular, with a slender keel and broad semi-membranous ciliolate margins. Inflorescence of 1–2 flowers from axils on young branches or from axillary short shoots up to 2 mm long on older ones; bracts of short shoots similar to stipules in size and shape; peduncles 11–17 mm long, jointed above the middle, finely puberulent, bearing a pair of bracteoles up to 1 mm long below the middle; flower (9–)11–13 mm long, strongly zygomorphic; calyx glabrous to sparsely puberulent, sepals 5, 2.5–3 mm long, lanceolate to ovate-lanceolate and acuminate to a sharp tip, herbaceous with narrow semi-membranous eciliate or ciliolate margins, the lateral pair of sepals slightly larger than the others; corolla white; petals 5, upper ones oblong-lanceolate and narrowly rounded to acutish at the tip, 3–4 mm long, lateral ones oblong-lanceolate to obovate and narrowly rounded at the tip, 4.0–4.5 mm long, bottom one (9–)11–13 mm long, at least twice as long as lateral and upper petals, slightly protuberant basally where it surrounds the glandular bottom stamens, narrowed in the basal half as a slender, longitudinally furrowed claw and expanded abruptly and broadly in the apical half to an ovate-triangular blade 5–7 mm broad, broadly acute to mucronate at the tip, broadly cuneate to subcordate at the base, the claw and base of the blade villous inside and puberulent outside; style not exerted at anthesis, 3–3.5 mm long, slender-cylindrical, gradually and uniformly expanding distally, abruptly bent to a short-conic tip; stamens 3–3.5 mm long, the filament up to one-fourth as long and one-third as broad as the anther proper, the ventral thecae together narrower than the anther body, tipped by an ovate-oblong, orange-brown connective appendage as long as or up to one-third longer than the anther body; the two bottom stamens 20% larger than the other three, on broader filaments bearing a dorsal gland, the dorsum of the anther glabrous or the bottom ones villosulous with a tuft of short white hairs on each side at the base; capsule narrowly ovoid, 8–9 mm long, glabrous, weakly veined, green when young but drying tan after dehiscence; seeds 2–3 per valve, ca. 3 mm long, obovoid to suborbicular, moderately lustrous, medium brown, lacking an elaiosome.

Habitat and phenology. While *Hybanthus hespericlivus* is distinct morphologically, geographically, and ecologically from other members of the genus in Mexico and Central America, plants are rather nondescript and do not lend themselves well to innovative descriptive names. The specific epithet "hespericlivus," or "western slope," was con-

cocted to characterize the peculiar mid-elevation distribution of the species along the northward extension of the cordillera in northwestern Costa Rica. This new species is restricted to mid-elevation mesic primary forest on the western slope of the cordillera in northern Costa Rica. Most collections have been taken from the general area of Volcán Rincón de la Vieja, especially in the valley between that peak and Volcán Miravalles. The species grows mostly between 1000 and 1100 m elevation but has been collected once at 800 m. Flowering from February to July, occasionally as early as November.

This species has a small primary geographic range in northwestern Costa Rica, excepting the single disjunct population east of the tip of the Nicoya Peninsula. Further collecting on mid-elevation west-facing slopes between the two portions of its bimodal range may reveal additional populations.

It is morphologically close to *Hybanthus sylvicola* of southern Mexico, Belize, Guatemala, and northern Honduras and somewhat less so to *H. jefensis* (the holotype of which was examined at MO), a narrow endemic of Cerro Jefe in central Panama. It differs from those species primarily in foliar and stipular characters as indicated in the key. Like *H. jefensis* in particular, *H. hespericlivus* remains relatively short, all collections being from plants 0.6–2 m tall. It grows at higher elevations than the others and inhabits primary montane forest rather than lower-elevation rainforest or premontane forest characteristic of *H. jefensis* and *H. sylvicola*. Although it has commonly been misidentified as *H. guanacastensis*, it resembles that species even less than *H. denticulatus*. Like *H. denticulatus*, it is immediately distinguished from that species by its larger and strongly zygomorphic flowers. Its foliage is also very different from that of *H. guanacastensis*. The two species are largely allopatric in distribution and elevation, the latter ranging almost entirely to the southeast and mostly at higher altitudes. A single collection from the Parque Nacional Rincón de la Vieja at 900–1200 m elevation (*Davidse et al.* 23430, MO) represents a putative hybrid of *H. guanacastensis* and *H. hespericlivus* with leaves and flowers intermediate in morphology and generally larger than those of either species.

Paratypes. COSTA RICA. **Alajuela:** 27.6 km NE of Liberia in forested pass area between Volcán Santa María and Volcán Miravalles, *Utley 5909* (DUKE, MO). **Guanacaste:** Parque Nacional Guanacaste, Estación Cacao, *Acovedo 29 & el curso II de Parataxónomos* (CR); Parque Nacional Guanacaste Estación Cacao, *Bello 2246* (INB); Parque Rincón de la Vieja, del puesto Santa María siguiendo el sendero del mirador, *Herrera 1561* (INB, WIS); Parque Nacional Guanacaste, Estación Mengo, *III INB 46* (CR); lower forested slopes of Volcán Orosí at the Hacienda Los Inocentes about 15 km SE of La Cruz, *Wilbur & Stone 10203* (DUKE). **San José:** In monte Aguacate, *Ørsted 647* (F).

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